# THE QUANTITATIVE DISTRIBUTION OF ABSORBING ROOTS OF *PINUS SILVESTRIS* AND *FAGUS SYLVATICA* IN A FOREST SUCCESSION

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## SUMMARY

This study describes the ecological significance of the spatial and quantitative distribution of absorbing roots during three stages in a forest succession, on the Margeride Plateau of the French Massif Central. The three stages represent natural establishment on degraded cultivations on stabilised granite solifluxion debris and are : (1) 10 year *Pinus silvestris* ; (2) 65 year *Pinus silvestris* with *Fagus sylvatica* understorey (3) 105 year *Pinus silvestris - Fagus sylvatica* mixed forest.

## RÉSUMÉ

Cette étude décrit la signification écologique de la distribution quantitative et spatiale des racines absorbantes durant trois étapes de l'évolution forestière sur le plateau de la Margeride, Massif Central (France).

Ces trois étapes de reconquête des cultures abandonnées sur des sols établis sur des arènes granitiques, sont les suivantes : 1. *Pinus silvestris* (10 ans d'âge) ; 2. *Pinus silvestris* (65 ans d'âge) à sous-bois de *Fagus sylvatica* ; 3. *Pinus silvestris* (105 ans d'âge) et *Fagus sylvatica,* en mélange.

## ZUSAMMENFASSUNG

Es wird die ökologische Bedeutung der quantitativen und räumlichen Verteilung der absorbierenden Wurzeln während drei forstlichen Entwicklungsstufen auf der Margeride-Hochebene (Massif Central, Frankreich) beschrieben.

Folgende Entwicklungsstadien wurden untersucht : eine zehn - jährige Pinus silvestris - Aufforstung ; Pinus silvestris (65 Jahre) mit Fagus sylvatica - Unterholz ; Pinus silvestris (105 Jahre) mit Buche gemischt.

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## INTRODUCTION

In studying forest succession and silviculture, the intensity of competition between trees is usually determined from measurements of crowns and trunks. Roots, because of their inconspicuous, subterranean nature are rarely considered but may also provide a quantitative measure of plant competition in forests. This paper examines root development in relation to tree competition, in three forest stages representing progressive reoccupation of abandoned cultivations, on the Margeride Plateau in the French Massif Central (McQUEEN, 1966). Variations in the quantity of roots judged to be absorbing are given and the relationships between root quantity and changes in tree canopy and soil examined.

Numerous investigations of root systems of trees are based on manual or hydraulic excavations of complete root systems. Inevitably many fine roots as well as mycorrhizae are lost during root excavation. These crude estimates have shown considerable variation in root distribution (LAITAKARI, 1927) as well as broad correlations between root development and factors such as trunk growth (HORTON, 1958), total subaerial volume (HOLSTENER-JØRGENSEN, 1959), and crown spread (MacMINN, 1963).

In some studies the quantity of fine roots has been determined by careful dissection of monolithic soil samples and related to above ground stand development (KALELA, 1949), water content of soil (SLAVIKOVA, 1958), and soil mineral nutrients (KERN *et al.*, 1961 ; ZÖTTL, 1964). In no study of fine roots has an attempt been made to seek correlations between the amount of fine roots and the photosynthetic parts of the crowns, even though the fine roots of forest trees appear to reflect both the growth of above ground tree parts and the edaphic conditions in which these roots grow. Whilst the quantity of fine roots, classed by diameter alone, has been measured, mycorrhizae have not previously been included as absorptive organs.

In this study, roots are classed in diameter ranges and grouped according to anatomical and morphological characters allowing external recognition of unsuberised tissues. Mycorrhizae and specified root types are combined to give the " absorbing root weight " or ARW. Consequently the ARW includes two organs of different absorptive capacity, particularly of phosphorus and of certain cations (HARLEY, 1959). The ARWs are compared with the crown volume (the space occupied by branches bearing green needles or leaves) and edaphic changes in the chronosequence of the three experimental sites.

## STAND DESCRIPTION

### 1. General.

The stands were on the Margeride Plateau of the French Massif Central, latitude ca. 44° 40′, longitude ca. 3° 40′ E. A wide range of ages of forest recolonisation of abandoned cultivations occurs (Long and Daget, 1965) but three sites as similar as possible, except for age of forest cover, were chosen for study. The three sites showed typical progressive change from the original pine *Pinus* stands to mixed pine and beech *Fagus* forest. The first stand was a dense pole stand of *Pinus silvestris* aged 10 years, the second an even-aged submature stand of *P. silvestris* of 65 years with an understorey of *Fagus sylvatica* and the third an even-aged, overmature stand of *P. silvestris,* of 105 years, with *F. sylvatica* co-dominant.

All stands were on gently sloping (1 %-4 %), north-west facing, old terraced cultivations. The underlying rock was a porphyroid granite, weathered to about 1 metre during the Pleistocene, to form a sandy grit (" arène ") of low clay content. This was subject to solifluxion during glacial periods and formed lobed terraces (Ph. Daget, pers. comm.) which have been modified by cultivation and strengthening with downslope walls.

The two sites of longer forest occupation adjoined the Commune of Thoras, the climate of which has been intensively studied and classified as microthermic, short summer (Daget et Poissonet, 1966). Climatological data and indicator species suggest the climate at the younger stand was similar to that at Thoras. All three sites occur at a vegatation boundary where a *Vaccinium myrtillus* vegetation changes to *Sarothamnus scoparius* below.

### 2. Vegetation.

Floristically and vegetationally the stands (1) parallel and complement those described by Long and Daget (1965).

The basal area of the pines increased slightly from 65 to 105 years while for *Fagus* the increase was ninefold (Table I). The trees became progressively taller

(1) Full descriptions are contained in McQueen (1966) and filed as C.E.P.E. releves Nos. 1268, 2229, 2230 at Montpellier.

TABLE I

*Average Stand Dimensions*

| | | No./ha | Basal Area dm²/ha | Top Height m | Radial increment over last 10 years cm | Depth of living crown m | Crown volume* 1000 m³/ha |
|---|---|---|---|---|---|---|---|
| Pinus | 10 | 26875 | – | 3,3 | 2,8 | 2,3 | 42,5 |
| Fagus | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Pinus | 65 | 1500 | 5022 | 14,5 | 0,99 | 5,5 | 28,7 |
| Fagus | 1-58 | 700 | 316 | 5,5 | 0,94 | 5,5 | 28,7 |
| Pinus | 105 | 800 | 5423 | 15,6 | 0,70 | 5,3 | 14,24 |
| Fagus | 1-100 | 600 | 2899 | 11,8 | 1,04 | 9,7 | 106,02 |

* Derived from the mean of eight equiangular radii of the green crowns and crown depth; as a cone and paraboloid respectively for Pinus and Fagus.

throughout the 105 years, with *Fagus* always forming a lower stratum. Whilst crowns of pines die below as the trees become taller, beech crowns persist below, possibly reflecting the greater shade tolerance of beech. By 105 years of age, the mean crown volume of beech per hectare was four times that of pine. Variations in crown volume might be expected to affect radial trunk growth (HALL, 1965) but the wood increment of the pine trees diminished between 65 and 105 years, even though the crown volume was constant.

## 3. SOILS.

LONG and DAGET (1965) consider the soils of a similar sequence to be biphasic ; " an inherited soil of cultivated origin, of the Brown Cultivated Soil type and a present day soil where the state of pedogenesis is dependent upon the vegetation... "

At all three stands the soil was fine textured, a silty to clayey sand in the A and B horizons, and a coarse sand in the C. Organic matter in the upper horizons increased between 10 and 65 years after which the $A_1$ horizon became progressively deeper.

Up to 65 years the litter would have been derived mainly from the pines and at that age the C/N of 26 for the $A_1$ horizon was high compared with 22 for the $A_1$ under a *Fagus* tree. Presumably more rapid decomposition occurs with

increasing amounts of beech litter and in the 105 year stand the C/N ratio was 20. Total soil exchangeable bases increased to 65 years of stand age after which this value remained more or less constant. After 65 years nutrient cycling apparently has reached equilibrium due to the presence of beech (FOGUELMAN, 1966) and base saturation was always below 20 % in the $A_1$ horizon of the 65 and 105 year stands. Physical parameters were also affected by the addition of organic matter ; thus total porosity at 10 years varied little in the profile (ca. 50 %) whilst at 65 and 105 years total porosity was about 75-80 % in the $A_1$, and 60 % in the B horizon.

## DISTRIBUTION OF ABSORBING ROOTS

### 1. SAMPLING METHODS.

KALELA (1955), found fine roots of *Pinus silvestris* were produced in greatest amounts between July and August. Since in this investigation most root samples were collected at the end of the growing season, and a few in early spring, the ARW values do not represent the maximum annual production of absorbing roots.

Examination of windthrown trees showed tree roots were largely confined to the upper 30 cm of soil and root sampling was confined to this depth. The large tree roots tended to flatten out on the surface of the C horizon.

Previous quantitative studies of fine roots have been based on sampling only in the interspaces between trees (KALELA, 1949 ; SLAVIKOVA, 1958 ; EHWALD *et al.* 1961 ; KERN *et al.*, 1961, and ZÖTTL, 1964). A system of " base of tree *versus* interspace " sampling was used, always under closed canopy and with the interspace sample points (" centres ") at maximum distances between each of four or five trees. In order to obtain more representative sampling, the absorbing roots were assumed to have distributions similar to larger roots with roots extending distances far exceeding the radius of crowns of trees (LAITAKARI, 1927 ; METRO and SAUVAGE, 1957) and a concentration at least of larger roots at the base of a tree (LAITAKARI, 1927 ; HORTON, 1958 ; MACMINN, 1963).

The mineral soil samples for root content were collected using a steel cylinder corer calibrated to collect a soil volume of 500 $cm^3$ including roots less than 2 cm diameter and fine roots in an *in situ* condition. For the organic horizons of the older stands soil samples were cut from a standard area.

All sampling was related to soil horizons, several samples from horizons less than 10 cm thick were taken to give 500 $cm^3$, and horizons greater than 10 cm

in thickness were subdivided in 10 cm intervals. The term " sampling layer " defines either complete or subdivided horizons.

The low organic matter content of the soil of the 10 year stand allowed easy breakdown and a water jet on a 2 mm sieve was used to separate roots from soil. Samples from older stands, containing up to 50 % organic matter, were soaked in 0.5 % NaOH overnight, and roots were separated from the soil by a root-washing machine (Cahoon and Morton, 1961) and the coarse mineral fraction ( 2 mm) retained for volume calculation of fine soil.

## 2. Root Identification.

The identification of roots and mycorrhizae was based on examination of root specimens from pure stands. Separation of living and dead roots was based on the degree of cohesion between cortex and periderm ; in the case of mycorrhizae, those still spongey were judged living. Suberised, unsuberised and mycorrhizal roots were identified from morphological characteristics for *Pinus, Fagus* and *Vaccinium myrtillus*. Suberised and unsuberised roots were distinguished by transverse sectioning from the apex until a distinct bark could be identified, Sudan IV being used as a diagnostic stain (Johansen, 1940). The appearance of suberin was then related to diameter and external morphology of the roots (Table II).

Table II

*Morphological characters used to identify root types*

| Species | Roots | | |
|---|---|---|---|
| | Suberised | Unsuberised | Mycorrhizae |
| *Pinus silvestris* | > 0,6 mm diam ; rough, twisted, grey bark, peeling off easily to reddish beneath, opaque. | 0,6 mm — 0,4 mm diam ; finely striate, white to dark brown ; slightly translucent. | Branching always dichotomous ; often forming compact spheroids up to 5 mm diameter, brown to black. |
| *Fagus sylvatica* | > 0,3 mm diam ; smooth ; gently curved ; outer bark generally well attached | 0,3 mm — 0,15 mm diam ; smooth ; white to reddish brown ; translucent. | Branching monopodial or sympodial ; loosely formed masses ; reddish brown to light yellow. |
| *Vaccinium myrtillus* | > 0,3 mm diam ; striate ; reddish ; straight ; complete bark peeling off during washing leaving white wood. | < 0,3 mm diam ; smooth ; reddish ; firmly attached to rhizomes or suberised roots. | (Endotrophic) |

The amount of fine, unsuberised roots and mycorrhizae expressed as oven dry weight per unit volume of soil, were assumed to give a valid index of current root activity even though other roots may be involved in nutrient and water uptake.

Although KRAMER (1956) cites field experiments in which water absorption by suberised roots was recorded during long dry periods, other experiments with radioactive tracers (WITHERSPOON, 1963 and YLI-VAKKURI *pers. comm.*) have shown $^{134}C$ and $^{32}P$ respectively are absorbed in greater quantities by unsuberised roots of *Quercus alba* and *Pinus silvestris* than by suberised roots. Mycorrhizae of *Fagus sylvatica* and *Pinus* spp. have a greater absorptive capacity than non-mycorrhizal roots for $^{32}P$, $^{42}K$ and $^{36}Rb$ (HARLEY, 1959). Furthermore fine roots unsuberised or only slightly so, seem sensitive quantitatively to edaphic factors (SLAVIKOVA, 1958 ; KERN *et al.,* 1961 ; ZÖTTL, 1964) but older suberised roots do not react in the same fashion.

KERN *et al.* (1961), and ZÖTTL (1964) found no correlation between quantities of fine ($<$ 0,5 mm diam.) and coarse tree roots ($>$ 0,5 mm). Since root weight determinations would have been accelerated if the weights of roots of different classes were correlated, root data for pine and beech were examined but no correlation existed. Considering unsuberised roots, mycorrhizae, and suberised roots less than 2 cm in diameter, from stands of 10 years and 105 years, the highest value of $r$ between any two classes was 0,6079 ($P < 0{,}001$) ; but few other values of $r$ reached significance at $P < 0{,}05$ and were infrequent and inconsistent. Consequently the combined oven-dry weight of unsuberised roots and mycorrhizae were used as the absorbing root weight.

## 3. THE 10 YEAR STAND.

Four randomly selected sampling stations were used in this stand. Initial storage difficulties entailed loss of samples and replications were not uniform with depth, an irregularity which precluded the use of a single analysis of variance. The data, being highly dispersed, were analysed in several steps.

Absorbing roots were distributed homogeneously in the soil layers (A) and (B) C′ at all four sampling stations in the stand. They occurred in greatest quantity in the (A) horizon (0-2,5 cm) and decreased significantly with depth (Table III). The mean ARW for each sampling layer was representative for the four stations, irrespective of position of sampling in relation to trees, and permitted valid comparisons on a profile/hectare basis with above ground measurements.

TABLE III

*Mean weights of absorbing roots in* 10 *years* Pinus *stand*

Values of P (FISHER & YATES, 1957) derived from analysis of variance and DUNCAN test (WEBER, 1964)

| Sampling layer | Depth cm | Area of sample $cm^2$ | Mean weights of absorbing roots mg/500 $cm^3$ | | kg/ha |
|---|---|---|---|---|---|
| | | | | P | |
| (A) | 2,5 | 201,04 | 496 | | 123 |
| | | | | 0,001 – 0,01 | |
| (B) C′ | 10,0 | 50,26 | 251 | | 499 |
| | | | | 0,001 – 0,01 | |
| (B) C″ | 10,0 | 50,26 | 125 | | 248 |
| | | | | 0,01 – 0,05 | |
| (B) C‴ | 10,0 | 50,26 | 60 | | 119 |
| Total | 32,5 | | 466 mg/litre | | 989 |

4. THE 65 YEAR STAND.

Past haphazard removal of pine trees from this stand considerably reduced the area available for sampling under closed canopy so fewer sampling stations could be used.

The three stations were located as follows ; at the base of a pine, of a beech and in the interspace furthest from neighbouring trees. At each station three complete soil profiles were taken, by three closely spaced replications of coring in each sampling layer. To test the differences in mean ARW for each station and each sampling layer the data were submitted to an analysis of variance with three factors : " Station ", " Depth ", " Species ". A positive relation with increasing depth, between means and standard deviations of ARW necessitated the logarithmic transformation of data.

No significant difference in ARW of either species occurred between sampling stations. For *Pinus* the mean ARW for the H and $A_1$ horizons was just significantly greater than for the B horizon but for *Fagus* there were no significant differences (Table IV). There was no significant difference between ARW of *Pinus* and *Fagus* in any sampling layer.

The roots of *Vaccinium myrtillus,* which were only a small fraction of the total absorbing root weight, were not included in the analysis of variance for the stand. Below *Pinus,* where the aerial cover of *Vaccinium* was greatest

TABLE IV

*Mean weights of absorbing roots in 65 years* Pinus *stand with* Fagus *understory*

Values of P derived from analysis of variance and DUNCAN test (n.s. = not significant). Between *Pinus* and *Fagus* the differences are not significant.

| Sampling layer | Depth cm | Area of sample $cm^2$ | Mean Weights of Absorbing Roots | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | *Pinus* | | | *Fagus* | | |
| | | | mg/500 $cm^3$ | | Kg/ha | mg/500 $cm^3$ | | kg/ha |
| | | | | P | | | P | |
| H | 1 | 250 | 429 | | 172 | 104 | | 42 |
| | | | | n.s. | | | n.s. | |
| A1 | 5 | 50,25 | 245 | | 244 | 167 | | 166 |
| | | | | 0,10 | | | n.s. | |
| B′ | 10 | 50,25 | 75 | | 149 | 210 | | 418 |
| | | | | n.s. | | | n.s. | |
| B″ | 10 | 50,25 | 35 | | 70 | 60 | | 119 |
| Total | | | 784 mg/2 litres | | 635 | 541 mg/litre | | 745 |
| | | | *Fagus* + *Pinus* 1289 mg/2 litres : 1380 kg/ha | | | | | |

(25 %), the absorbing roots of this species were distributed uniformly in the H, $A_1$, and B′ sampling layers (from 0-16 cm).

## 5. THE 105 YEAR STAND.

Three replicated profiles were taken at each sampling station as in the 65 year stand, but sampling was more extensive. Sampling stations were at the base of two *Fagus* trees, two *Pinus* trees and three ‘ centres ’.

The ARW values from individual samples were highly dispersed and it was necessary to test statistically the significance of apparent differences between means by an analysis of variance. As the means and standard deviations of ARW for both species were a function of depth, in direct relation to each other, the data were logarithmically transformed.

The weight per volume of soil of absorbing roots for *Fagus* was always significantly greater than for *Pinus* (Table V). Pine absorbing roots were most abundant in the two superficial layers, whilst beech absorbing roots occurred uniformly through the profiles, as at 65 years.

TABLE V

*Mean weights of absorbing roots in mixed stand of* Pinus 105 *years and* Fagus.
Values of $p$ derived from analysis of variance and DUNCAN test. (n.s. = not significant).
Between *Pinus* and *Fagus* the difference is highly significant at $P < 0{,}001$.

| Sampling layer | Depth cm | Area of sample $cm^2$ | Mean Weight of Absorbing Roots | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | *Pinus* | | | *Fagus* | | |
| | | | mg/500 $cm^3$ | | kg/ha | mg/500 $cm^3$ | | kg/ha |
| | | | | P | | | P | |
| H | 2 | 250 | 123 | | 49 | 482 | | 193 |
| | | | | n.s. | | | n.s. | |
| A1 | 10 | 50,25 | 78 | | 155 | 593 | | 1179 |
| | | | | 0,01 — 0,005 | | | n.s. | |
| B′ | 10 | 50,25 | 39 | | 77 | 351 | | 698 |
| | | | | n.s. | | | n.s. | |
| B″ | 10 | 50,25 | 18 | | 36 | 167 | | 332 |
| Total | 32 | | 129 mg/litre | | | 796 mg/litre | | 2402 |
| | | | *Fagus* + Pinus 925 mg/litre : 2720 kg/ha | | | | | |

The mean ARWs for pine, in all horizons, do not vary significantly between stations in the 105 year stand, but beech roots are concentrated near the trunk at two stations of the seven. Trial correlations showed no discernible relationship between individual crown volumes and root weights from profiles at the bases of individual beech trees.

## CHANGES IN ABSORBING ROOTS WITH TIME

The evolution of the fine root system in the three stands (Fig. 1) was associated with changes in forest composition and soil profile morphology. Between 10 and 65 years the ARW for *Pinus* in the A horizons decreased, but considering the development of the two upper horizons together, the combined root content of (A) and (B) C′ layers at 10 years and of the H and $A_1$ at 65 years, was relatively constant. KALELA (1949) found the length of fine roots (< 1 mm diam.) per volume of soil increased until 90 years of stand age but he was studying pure *P. silvestris* forest, not a mixed pine and beech stand.

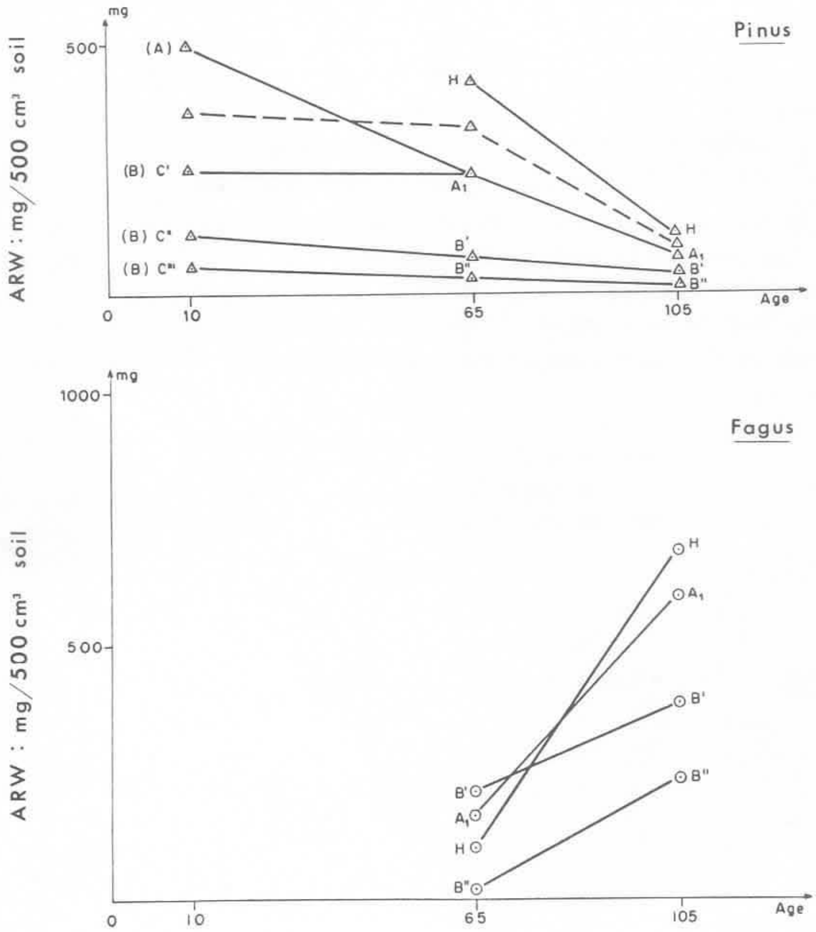


FIG. 1. — Development of absorbing root occupation of soil horizons with increasing forest age. For *Pinus* (- - -) indicates mean ARW for two upper horizons.

| 10 years | 65 years | 105 years |
|---|---|---|
| $A_1$ = 2,5 cm | H = 1 cm | H = 2 cm |
| (B) C′ = 10 cm | $A_1$ = 5 cm | $A_1$ = 10 cm |
| (B) C″ = 10 cm | B′ = 10 cm | B′ = 10 cm |
| (B) C″ = 10 cm | B″ = 10 cm | B″ = 10 cm |

The absorbing roots of *Fagus* at 65 years were uniformly distributed throughout the profiles ; at 105 years they tended to be concentrated in the H and $A_1$ horizons, although this concentration was not significant statistically.

While the quantity of absorbing roots per profile/hectare remained relatively constant between the 10 and 65 years (Fig. 2) the total weight of absorbing roots, (*Pinus* + *Fagus*) increased considerably. EHWALD *et al.* (1961) found a similar increase in combined weight of *Fagus sylvatica* and *P. silvestris* roots (< 2 mm diam.) between 68 and 90 years stand age.

The increase in amount of *Fagus* absorbing roots with time (Figs. 1 and 2) causes the increase in total root weight. KERN *et al.* (1961) found a greater weight of fine roots (< 0,5 mm diam.) in mixed forests of conifers and *Fagus sylvatica* than in pure stands of the same age. They also found more *Fagus* fine roots than conifer roots in the lower soil horizons of mixed stands, as in this investigation.

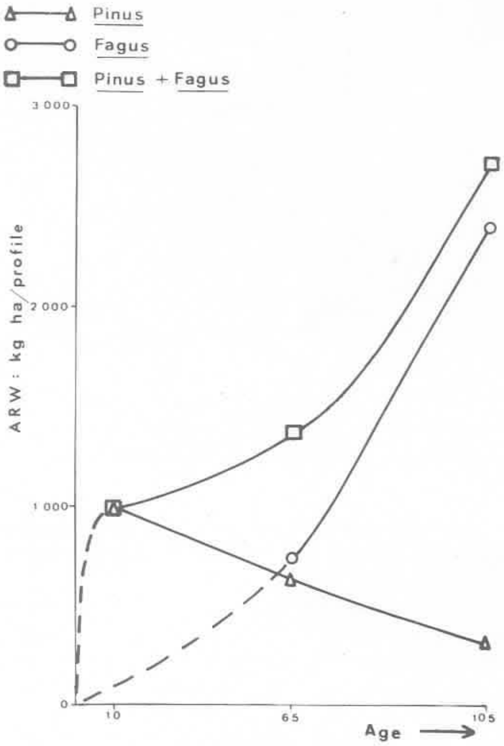


FIG. 2. — Absorbing root weight per hectare/profile (right) for stands of 10, 65 and 105 years.

## INTERSPECIFIC RELATIONS BETWEEN ABSORBING ROOTS

At 65 years the amount of beech absorbing roots equals that of *Pinus,* and these are uniformly distributed through the soil profile. At 105 years the distribution of Fagus absorbing roots has not changed, but the amount has increased whilst the weight of *Pinus roots* has decreased.

Morphological differences between absorbing roots of the two species have two important effects :

(1) The absorbing roots of *Fagus* ramify throughout the lower soil horizons, and their fineness (< 0,3 mm diam.) seems advantageous for penetration of the soil of the B horizon, where total porosity is low. The pine absorbing roots were virtually restricted to the H and $A_1$ horizons. Since the beech roots were distributed throughout the soil they would be able to exploit deeper resources of soil moisture during dry periods and to utilise more fully nutrients leached from the H and $A_1$ horizons.

(2) The H and $A_1$ horizons in the 65 year stand, were equally occupied by roots of *Pinus* and *Fagus*. Forty years later, the ratio between the roots of the two species was heavily in favour of *Fagus*. Beech roots have a greater potential absorptive surface per unit dry weight than pine roots because they are finer and so can better exploit the superficial soil horizons.

## ABSORBING ROOTS AND CROWN VOLUME

The shoot/root ratio of tree seedlings tends to be constant under uniform environmental conditions (KRAMER and KOZLOWSKI, 1960). Similar ratios for adult trees have been inferred by HOLSTENER-JØRGENSEN (1959), based on entire major root systems correlated with entire subaerial parts of trees. MACMINN (1963), suggested the spread of root systems of *Pseudotsuga menziesii* was related to crown spread rather than to trunk volume.

Extensions of the shoot/root ratio from young seedlings to adult trees would be more valid if based on the quantity of absorbing roots and the quantity of actively photosynthesising organs ; rather than including the accumulation of secondary tissue of larger roots, trunks and branches.

For both pine and beech there was a relatively constant shoot/root ratio between crown volume/ha and absorbing root weight/ha/profile (Fig. 3). Since the average diameter of absorbing roots of beech was less than for pine, for the same weight of roots the absorbing surface would be greater for beech.

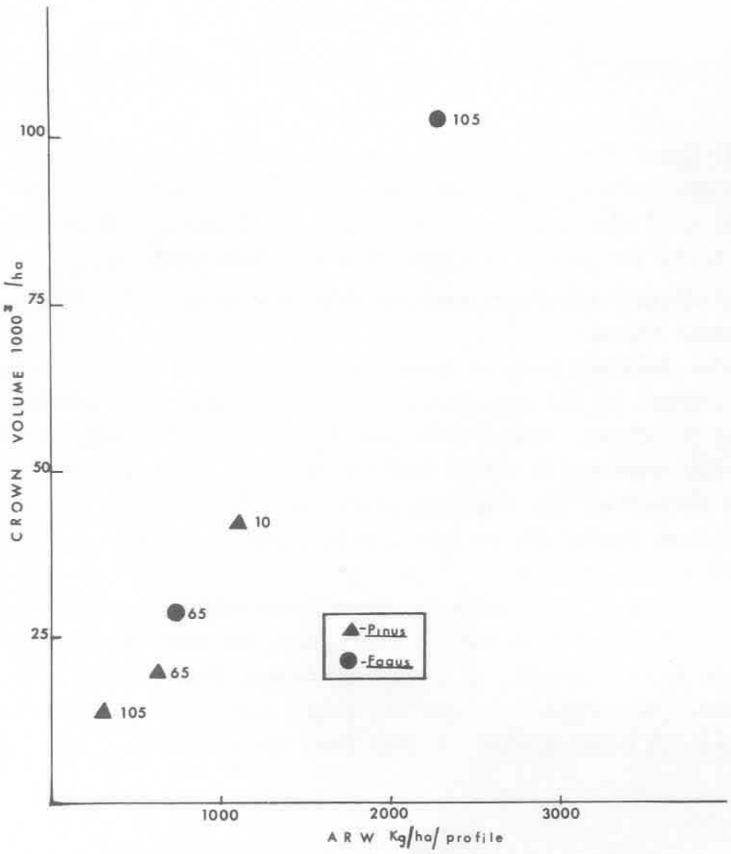


FIG. 3. — Comparison of absorbing root weight (ARW) per hectare/profile ca. 30 cm depth, and crown volume per hectare for *Pinus silvestris* and *Fagus sylvatica*. Stand ages are indicated beside the points.

## ABSORBING ROOTS AND EDAPHIC CHARACTERS

Comparison of volumes of coarse soil particles (2-80 mm) and the respective ARWs for 140 random samples gave no significant relationship ($r < 0{,}1\ 000$). At 10 years stand age no consistent relation existed between total soil porosity and pine ARW but at 65 and 105 years, porosity and ARW were related though differently for each profile and age sampled. The quantity of beech roots was independent of soil porosity, the finer diameter of *Fagus* absorbing roots (< 0,3 mm) probably helping their penetration of low porosity soils (WIERSUM, 1957). SCHUURMAN and GOEDEWAGEN (1956) working with wheat and LEIBUNGUT

(1963) with trees, suggested that 40 % total soil porosity was the threshold barrier to root growth and in the soils studied here the total porosity was never less than 50 %. The absorbing roots of beech are distributed through all horizons, irrespective of porosity variations and *Pinus* roots are concentrated in the upper horizons.

Comparison of the quantity of pine absorbing roots and soil organic matter (per volume of soil) showed a very slight positive linear relation at 10 years but a loose curvilinear relation at 65 and 105 years irrespective of stand age or horizon. Organic matter variations apparently had no effect on quantities of beech roots.

## DISCUSSION

The ARWs for *Pinus* at 65 and 105 years were positively related to total soil porosity, but to different degrees in each profile. *Fagus* roots were distributed evenly through the whole profile, the intrinsic fineness of *Fagus* roots probably contributing to penetration of the less porous horizons.

At 65 and 105 years, the absorbing roots of *Pinus* were positively related to amount of organic matter, a relation continuous through several profiles and the two ages, suggesting a nutritional effect rather than direct amelioration of soil physical conditions by added organic matter. The absence of any relation between the absorbing roots of *Fagus* and organic matter may be due to physiological differences in the absorptive mechanisms between the two species, probably located in the mycorrhizae. Mycorrhizae of both species (HARLEY, 1959) absorb nutrients from organic matter.

At 10 years the absorbing roots of *Pinus* showed only slight, or no relation to the various soil characters examined. Probably the success of *Pinus* as a coloniser of nutritionally degraded and compact soils, is due to the comparative robustness of roots (diam. 0,4-0,6 mm) and their equally robust mycorrhizal development. Both are characters favourable to the establishment of an active root system in the top 10 cm of virtually unprotected soil, which in summer becomes extremely dry. Although total soil porosity is low in this layer, the unmeasured macroporosity ($> 150\ \mu$) could be considerable, particularly as rain eluviation of fine soil particles is common in these soils (LONG and DAGET, 1965).

By the time a layer of organic matter has developed the *Pinus* canopy is clear of the ground and sufficient light penetrates the canopy to permit beech to become established. When beech invades the *Pinus* stand, its shade tolerant crown of greater photosynthetic area than that of *Pinus* allows production of a greater

quantity of roots. Their roots, being finer also, penetrate into the less porous lower horizons in greater quantity than those of *Pinus*. Pine roots remain superficial remaining in the horizons of greater organic matter content.

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